Reference: *Biol. Bull.* **161**:236–245. (October, 1981)

HISTOLOGY OF A BILATERAL GYNANDROMORPH OF THE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN (DECAPODA: PORTUNIDAE)

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Abstract

The anatomy and histology of a gynandromorphic blue crab, *Callinectes sapidus*, are described. This is the first bilateral gynandromorph reported in a species of the Brachyura. Externally there was perfect bilateral division into male and female sides. The gonad on the male side was morphologically and histologically normal, but an AVD (anterior vas deferens) had been differentiated on the female side, and spermatogenesis was occurring through much of the female gonad. However, oogenesis was taking place in the apical portions of the gonadal lobes and a normal seminal receptacle was present. The crab had copulated as a female and may have copulated as a male.

Function of the malacostracan AG (androgenic gland) in control of maleness is discussed. It is concluded that sexual differentiation in malacostracan species exhibiting bilateral gynandromorphism must depend on complex mechanisms. External sexual characters may be determined very early in embryogenesis, but differentiation of the gonads is apparently influenced by the AG and other parts of the hormonal systems.

Introduction

A blue crab, *Callinectes sapidus* Rathbun, that displayed perfect external bilateral gynandromorphism, was taken from a tributary of Chesapeake Bay. It has been briefly described by Otto (1979). This apparently is the only blue-crab gynandromorph that has been brought to the attention of scientists concerned with the species, and is the only bilateral gynandromorph reported in the Brachyura. Considering that blue crabs have been fished commercially for many years, especially in the Chesapeake Bay region, and that male and female blue crabs are easily distinguished externally, one must conclude that bilateral gynandromorphism is extremely rare in this decapod species. The rarity of externally evident gynandromorphism of any kind in dioecious (nonhermaphroditic; gonochoristic) decapods is further demonstrated by the facts that Hartnoll (1960) found only one gynandromorphic *Hyas coarctatus* of 2500 examined, George (1963) reported one gynandromorph among 16,870 specimens of *Metapenaeus monoceros,* and Farmer (1972) discovered but one gynandromorph in the 40,000 specimens of *Nephrops norvegicus* he examined.

Functional and nonfunctional hermaphroditism occurs in several groups of malacostracan crustaceans, but gynandromorphism apparently is confined to the Decapoda. Farmer (1972) and Charniaux-Cotton (1975) believe that bilateral gyn-

Received 1 July, 1981; accepted 29 July, 1981.

Abbreviations: AG, androgenic gland; AVD, anterior vas deferens; MVD, median vas deferens; PVD, posterior vas deferens.

andromorphism in decapods is of genetic origin. It could be due to loss of a chromosome during early embryogenic cleavage. If the initial embryonic cleavage were determinate, a single abnormal division involving sex chromosomes would be sufficient to cause the condition.

Partial gynandromorphism has been observed in species of macrurans, anomurans, and brachyurans (see Hartnoll, 1960, and Charniaux-Cotton, 1975), but the literature mentions occurrence of bilateral gynandromorphs only in species of macrurans. Based on the literature and his own investigations, Farmer (1972) listed the following cases: two specimens of *Homarus gammarus,* two of *Homarus americanus,* two of *Nephrops norvegicus,* and one of *Palinurus frontalis.* The internal anatomy was investigated in one specimen each of *N. norvegicus, H. gammarus,* and *H. americanus.* In these three animals, division of the gonads into testis-vas deferens and ovary was also bilateral and corresponded to the external condition. The one gynandromorphic *N. norvegicus* examined histologically had mature sperm in the testis and large oocytes in the ovary. Both testis and ovary appeared normal (Farmer, 1972). One gynandromorphic *H. americanus* was also examined histologically. This lobster had mature sperm in the testis and vas deferens; the ovary contained maturing ova and some possibly degenerate ones (Chace and Moore, 1959). Neither Farmer (1972) nor Chace and Moore (1959) mentioned whether vitellogenesis was occurring in their specimens, but because they speak of large and maturing ova, presumably it was. The AG (androgenic gland) was not searched for in either specimen.

It is believed that all malacostracan crustaceans have AGs. Expression of primary and secondary sexual characters of the male is controlled by the AG in species of amphipods, isopods, and protandric hermaphroditic natantian decapods that have been studied. If young females receive AG implants, the ovaries transform into testes and external male characteristics develop with successive molts. Conversely, males deprived of AGs develop ovaries and female secondary characters (Charniaux-Cotton, 1975). Because early experiments with AG implants and ablations in dioecious brachyuran decapods were only marginally successful in modifying sexual characters, it was thought that expression of sex in dioecious decapods might differ from its expression in amphipods, isopods, and protandric decapods (Payen, 1969; Charniaux-Cotton, 1975). Recently, however, females of two dioecious species of natantians were masculinized by AG implants. Partial masculinization was obtained in *Palaemonetes varians* (Charniaux-Cotton and Cazes, 1979) and complete masculinization in *Macrobrachium rosenbergii* (Nagamine *et al.,* 1980b). Nagamine *et al.* (1980a) also induced feminization of young *M. rosenbergii* males by ablating the AGs.

The bilateral gynandromorph of the blue crab offered an opportunity to investigate histologically the condition of the gonads and other organs in a dioecious brachyuran whose external secondary sexual characters were unequivocally male on one side and female on the other, and to assess the histological data in the light of the recent results of AG implantation and ablation in the dioecious natantian decapods mentioned above.

Materials and Methods

The gynandromorphic blue crab was taken on 10 July 1979 in a commercial crab trap set in Broad Creek (a tributary of Chesapeake Bay), Talbot County, Maryland. It was maintained out of water for the remainder of that day and transported on ice to the Oxford Laboratory the following morning. It was moribund

when received and dead when it was dissected in the early afternoon. The owner of the crab had requested that the ventral and lateral parts not be damaged during dissection. Therefore, only the median part of the carapace was removed, and neither the AGs nor the Y organs (molting glands) could be taken.

On the male side of the crab, samples were taken of the AVD (anterior vas deferens), MVD (median vas deferens), PVD (posterior vas deferens), and of the testis, both proximal to the AVD and as near the anterior tip of the testis as possible. On the female side, four samples were taken of the gonad; the first was from near the AVD, the second from the median area of the anterior lobe, the third from the apical part of the anterior lobe, as near the tip as possible, and the fourth from the most distal part of the posterior lobe. The entire seminal receptacle was taken. Other tissues and organs sampled included the entire brain and thoracic ganglion, and parts of the hepatopancreas, midgut, midgut ceca, hemopoietic tissue, antennal gland, epidermis, gill, mandibular organ, and heart (see Johnson, 1980).

The tissues were fixed in Helly's fluid, dehydrated, and embedded in paraffin in the usual manner. Tissue sections were stained with hematoxylin-eosin, with alcian blue-nuclear fast red, and by the periodic acid-Schiff and Feulgen techniques (Johnson, 1980).

Results

External anatomy

The crab was large (18 cm carapace width) and in good condition. The exoskeleton was hard, but free of blemishes, indicating that the animal had molted relatively recently. External sexually dimorphic characters were male on the right side and female on the left side (Figs. 1, 2). The male cheliped was blue and larger than the female cheliped, which was red tipped, as is typical of female blue crabs. The anterolateral margin of the carapace was less convex on the male side. The male half of the abdomen was narrow; the female half was broad, with the convex lateral margin of a mature female (Fig. 2). The pleopods had the male form on the right and female form on the left (Fig. 3).

Internal anatomy

All the internal organs, except the gonads, were of normal appearance. As in normal blue crabs, the gonads formed an "H," with an anterior and a posterior lobe on each side and a central crossbridge posterior to the stomach.

On the male side, a slender testis extended anterolaterally as far as it could be followed. The coiled white AVD occupied its normal position close to the median bridge, and was of the usual size. When it was cut, numerous spermatophores escaped from its lumen. The MVD was also in its usual position, being somewhat lateral to the AVD, and partly obscured by it. It was pinkish and much smaller than would be expected in a normal male that had not copulated recently. The PVD was of the normal greenish, translucent color and ran posteriorly in the ventral part of the body cavity. Unlike the PVD of a normal mature male that has not copulated recently, it was not bulbous and distended with secretion, but was tubular and with a variable diameter that did not greatly exceed the diameter of the midgut in most parts.

On the female side, the anterior lobe of the gonad was white and about the same diameter as the testis. Proximal to the crossbridge of the gonad was a white,

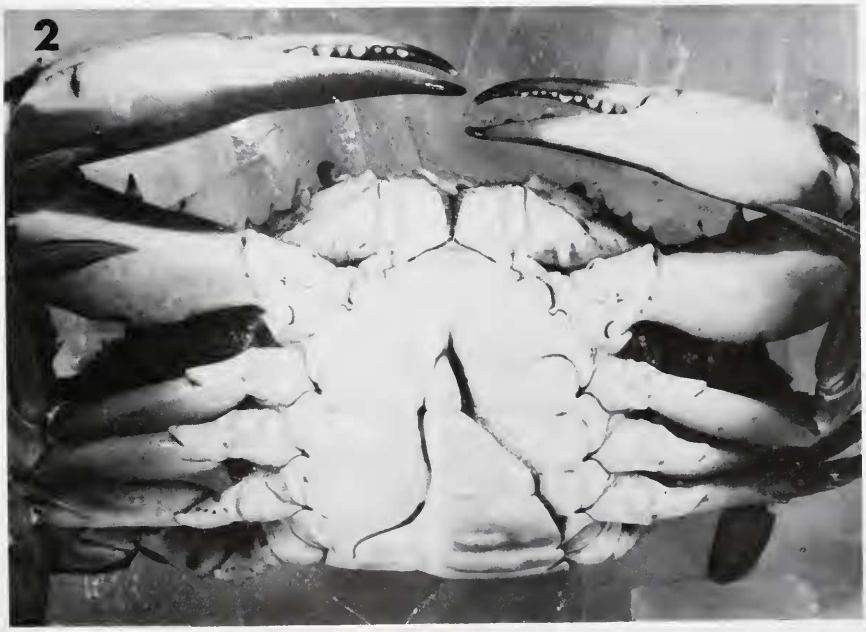

FIGURE 1. Dorsal view of the gynandromorph; male to right, female to left.
FIGURE 2. Ventral view of the gynandromorph; male to left, female to right.

coiled, tubular part that appeared like, and occupied the usual position of the AVD. It was a functioning AVD, as demonstrated by the release of spermatophores when it was cut. There was no sign of an MVD or a PVD. The posterior lobe of the gonad was very slender, white, and difficult to follow. It did not differ in appearance

from the posterior ovarian lobe of an immature female, or the testicular lobe of a young male. Like the posterior lobe of the normal ovary, it was dorsal and ended posteriorly in the region of the posterior midgut cecum. The seminal receptacle of the blue crab is white, except for a variable period following copulation. At that time, it is enlarged and pink, due to presence of the pink sperm plug. The seminal receptacle of the gynandromorph was small and flat, but it was pinkish, indicating retention of a part of the sperm plug.

Histological appearance

The internal organs and tissues appeared normal except for the gonads. The crab was in intermolt (stage C). Neurosecretory cells of the brain and thoracic ganglion were morphologically similar on the two sides. The crab was well nourished. There was considerable glycogen in the spongy connective tissues; and the reserve-inclusion cells, that store hemocyanin and other materials and are associated with the connective tissues and hepatopancreas, were normal in size and number. The hepatopancreatic tubules and the antennal gland were autolysing. Other tissues showed little or no degeneration, except that the midgut epithelium had fragmented and sloughed into the lumen, and mitosis in the hemopoietic tissue was arrested in prophase. Most of the prophase nuclei were pyknotic. There was no evidence of microbial or parasitic infection except for three degenerate gregarines in the lumen of the posterior midgut cecum.

Testicular lobules on the male side contained primary and secondary spermatocytes, spermatids, and developing sperm. All the cells in a single lobule were in one developmental stage, as typical of mature blue-crab males. Few gonia (stem cells) were visible in the sections, and mitosis was rare. Some primary spermatocytes were in prophase, but the nuclei appeared to be pyknotic (Fig. 4). There were many mature sperm in the seminiferous duct.

The AVD had a normal, thick epithelium. Both forming and fully encapsulated spermatophores were present in the lumen, surrounded by the usual heterogeneous secretion. Epithelia of the MVD and PVD had the large, lobed nuclei typical of mature males. Lumina of the MVD and PVD contained secretions typical of the particular part of the vas deferens, but neither part was greatly distended with secretion, and outpocketings from the main lumen were evident (Fig. 5).

On the female side, adjacent to the crossbridge and the abnormally present AVD, the gonadal lobules contained primary spermatocytes (Fig. 6), and just distal to this portion, lobules were filled with primary spermatocytes, spermatids, and developing sperm. As on the male side, each lobule contained cells in a single stage of development. Proximal to the AVD, the seminiferous duct was thick walled (Fig. 6), and resembled the normal male seminiferous duct near its entrance into the AVD. In the median part of the anterior lobe of the gonad, most lobules contained secondary spermatocytes. There were few gonia and no spermatids or developing sperm in sections of the median sample, but the seminiferous duct here was full of mature sperm. In most cross sections, the seminiferous duct had a columnar epithelium around the entire circumference, rather than having one side opening broadly into a lobule, as it does in normal testis. The distal part of the anterior lobe of the gonad contained oocytes and a few gonia. The oocytes were like those of females just before and after the pubertal molt. Many of the larger ones contained "yolk nuclei," which are considered indicators of impending vitellogenesis (Cronin, 1942; Johnson, 1980). There were fewer oocytes per lobule than normal, and they were broadly separated by cytoplasm that presumably belonged to the accessory

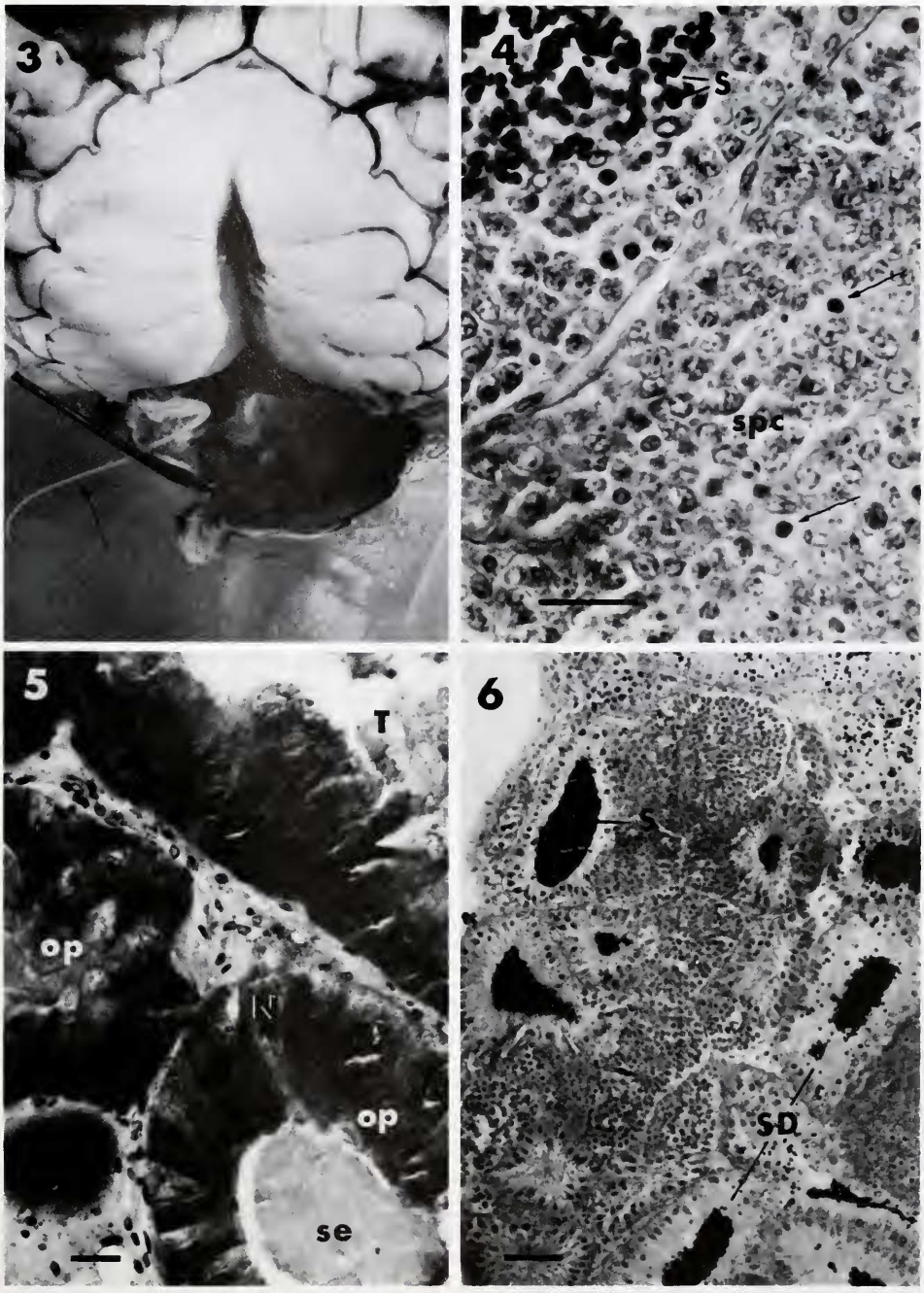

FIGURE 3. Venter of abdomen of the gynandromorph. Note long first pleopod on the male side (arrow).

FIGURE 4. Testicular lobules on the male side. Arrows point to arrested mitoses. Periodic acid-Schiff. spc = primary spermatocytes; S = sperm. Bar = 20 μm.

FIGURE 5. PVD on the male side. Hematoxylin and eosin. N = nucleus of PVD epithelium; op = outpocketing from main tubule; se = secretion in lumen; T = main tubule. Bar = 20 μm.

FIGURE 6. Testicular lobules on the female side, near the AVD. Lobules contain primary spermatocytes. Note the thick epithelium of the seminiferous duct (SD) and the sperm (S) within it. Periodic acid-Schiff. Bar = 50 μm.

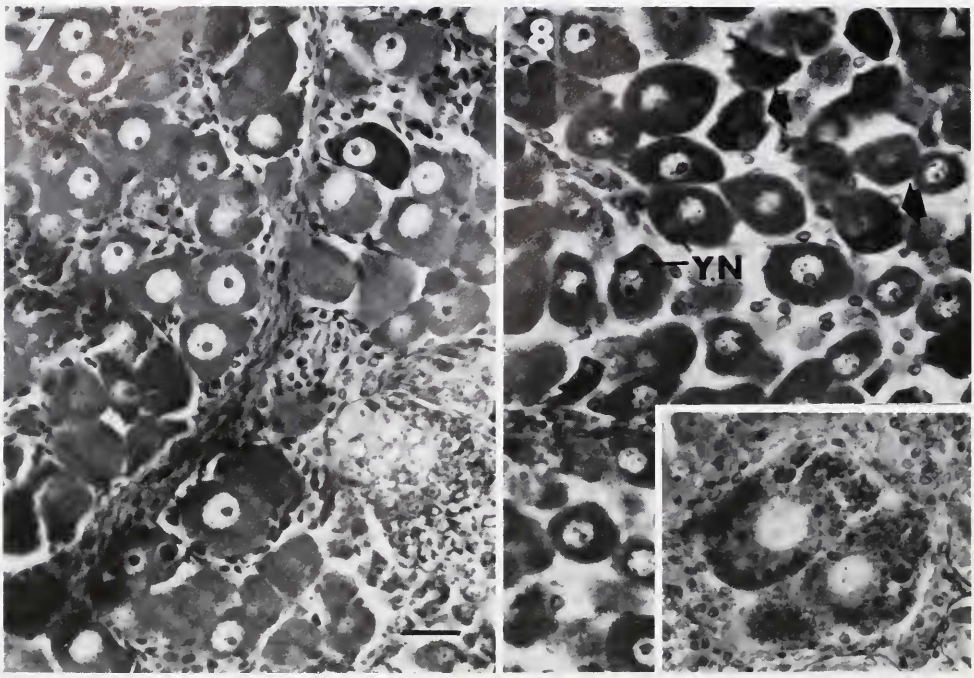

FIGURE 7. Ovarian lobules from a normal, molting, pubertal female. Periodic acid-Schiff. Bar = 20 μm.

FIGURE 8. Ovarian lobule from the posterior gonadal lobe on the female side. Arrows point to degenerating oocytes. Hematoxylin and eosin. Inset: vitellogenic oocytes from the anterior gonadal lobe on the female side. Periodic acid-Schiff. YN = yolk nucleus. Same scale as Figure 7.

(follicle) cells (compare Figs. 7 and 8). Degenerating oocytes were more common than in normal crabs. In one small area, several oocytes were undergoing early vitellogenesis (Fig. 8, inset). The apex of the posterior lobe of the gonad contained previtellogenic oocytes similar to those in the tip of the anterior lobe. Oocytes undergoing vitellogenesis were not seen in the posterior apex.

The seminal receptacle appeared like that of a mature female. The lumen was open and the more dorsal portions of the epithelium had sloughed into the lumen. A remnant of the sperm plug was present in the ventral part of the lumen, and a few sperm were associated with it.

DISCUSSION

It was not possible to search for the AG during dissection of the gynandromorph. If differentiation of male sexual characters of the blue crab is partially or wholly dependent on presence of the AG, one must have been present in the gynandromorph, at least until male puberty. Partial differentiation of the gonad on the female side into an AVD and a functioning testis indicates that the AG may have been functional at the time of death.

Ablation of the AG causes an inhibition of spermatogenesis in the dioecious natantians *Crangon* and *Leander,* and a hormone produced by the protocerebrum is necessary for maintenance of spermatogenesis (Touir, 1977a, b, c). Because there

were large numbers of spermatophores and mature sperm in the testis and AVD of the blue-crab gynandromorph, lack of mitoses in its testicular lobules probably was not due to the possible lack of an AG or disturbance of protocerebral hormones, but because of the impaired physiological condition of the crab. It had been stressed by being out of water for at least 24 h, and had been kept at low temperatures for a part of that time. Cessation of mitosis in the hemopoietic tissue, and probable premortem termination of function in the hepatopancreas, midgut, and antennal gland also indicated physiological dysfunction.

Reasons for reduced secretion in the MVD and PVD were not readily evident. The condition of the epithelial nuclei, which were large and lobed, indicated that the MVD and PVD were in a fully secretory state. The crab may have recently copulated as a male. During copulation, secretion is expelled from the MVD and PVD and they contract, resulting in outpocketings from the main lumen like those in the gynandromorph (Johnson, 1980). However, the AVD of the gynandromorph contained many spermatophores. Usually, after copulation in a normal male, very few spermatophores remain in the AVD. The possibility exists that reduced secretion may have depended on interference with function of the AG or other parts of the male hormonal system, rather than on recent copulation.

The AG's influence on sexual behavior of crustaceans has not been studied. Sperm were in the seminal receptacle of the gynandromorph, and a portion of the sperm plug remained in the receptacle, showing that copulation with a male had occurred following the female pubertal molt. The male blue crab carries the prepubertal female during her premolt stage and copulates with her directly following molt. Except for prepubertal females, blue crabs exhibit agonistic behavior during premolt (Johnson, personal observation). For the crab to have copulated as a female, agonistic behavior regulated by the male side of the premolt gynandromorph would have had to have been overridden by the female behavior pattern. Few sperm were in the seminal receptacle, indicating that copulation had not been completely successful. Probably the presence of a male morphology on one side of the crab had interfered with the normal procedure.

Male hormones had influenced the remaining ovarian tissue on the female side. Early vitellogenesis should have been evident in most oocytes of this mature stage C blue crab (Johnson, 1980), but only one small group of oocytes was vitellogenic, and degenerating oocytes were rather common. The influence of the AG hormones may have been responsible; Payen (1969) reported that AG implantation inhibited vitellogenesis in one of 29 implanted females of another brachyuran, *Rhithropanopeus harrisii.* Neurohormones produced in eyestalk and thoracic ganglia of the crabs *Potomon* and *Eriocheir* influence reproductive condition of females, and increased activity is evident in certain neurosecretory cells of the thoracic ganglion during the reproductive period (Demeusy, 1970). Secretory activity was not morphologically evident in neurosecretory-cell groups on either side of the thoracic ganglion and brain of the blue-crab gynandromorph.

Charniaux-Cotton (1975) summarized the differences between sexual determination in amphipods, isopods, and hermaphroditic natantian decapods on the one hand, and dioecious decapods on the other. She postulated that genes in the first group allow expression of either male or female characters, that the AG is present only in genetic males, and that expression of male characters is brought about by AG hormones. In the second group, experiments to that date indicated that sexual differentiation depended on local inducers, rather than on circulating androgenic hormone produced by the AG, although Charniaux-Cotton considered the AG to be important in regulating changes that occur at puberty. The above

concept must be modified because, as mentioned earlier, AG implants cause external masculinization of *P. varians* (Charniaux-Cotton and Cazes, 1979) and complete masculinization of *M. rosenbergii* (Nagamine *et al.*, 1980b); while ablation of the AG causes complete feminization of very young *M. rosenbergii* males (Nagamine *et al.*, 1980a). There is an inverse relationship between the degree of masculinization and the age of the animal at the time of AG implantation in females of *M. rosenbergii* and the various amphipods and isopods studied (Nagamine *et al.*, 1980b). Nagamine and co-workers concluded that earlier attempts to masculinize female decapod crustaceans failed, in part, because there was an insufficient number of molts between AG implantation and termination of the experiments. They also concluded that recently differentiated gonadal systems of both sexes of *M. rosenbergii* and probably other malacostracans are labile, but with age become progressively determined toward the genetic sex of the individual. Therefore, AG implantation in older females would lead to no or only partial masculinization, particularly if the animals molted infrequently.

The existence of bilateral gynandromorphs in species of macrurans and brachyurans shows that sexual differentiation in species capable of gynandromorphism must be either governed differently than in *M. rosenbergii,* or the presence in bilateral gynandromorphs of all the hormonal systems governing expression of sex gives a different final result than artificial presence of the AG alone in genetic females, or artificial absence of AG alone in genetic males. Farmer (1972) emphasized that if the AG of lobsters acted like that of amphipods, isopods, and protandric natantians in controlling maleness, a single AG in a bilateral gynandromorph should not only transform the ovary into a functional testis, but also at least reduce the contrast of external female characters on one side with external male characters on the other side. He suggested that a degree of determinism in the early embryo may be more common than previously thought. Because the AG is present as a morphological entity in male blue crabs at the sixth post-larval molt (Payen *et al.*, 1967), hormones from the AG presumably were present then and later in the gynandromorphic blue crab. Nonetheless, external sexually dimorphic characters were retained fully by the female half even through the pubertal molt. Further, in a gynandromorphic *H. americanus* the gonad adjacent to the crossbridge contained oocytes on the male side (Chace and Moore, 1959). This section completely separated the anterior and posterior lobes of the testis, suggesting a slight dominance of the female hormonal system. In the gynandromorphic blue crab, androgenic hormonal systems were internally dominant. Not only was spermatogenesis taking place through much of the gonad on the female side, but an AVD had been differentiated and vitellogenesis was apparently inhibited.

The existence of bilateral gynandromorphs demonstrates that masculinizing action of the AG in *Homarus, Nephrops,* and *Callinectes* must be tempered by other parts of the hormonal systems, and possibly by early determinism. Eventual form of externally expressed sexual characters must be decided very early during morphogenesis in these genera. The morphological development of the animals before their capture is not known, but their final morphological condition shows that mature external female characters are expressed on the female side despite the presumed presence of androgenic hormones during most or all of development. Gonadal differentiation in the gynandromorphs was apparently more easily influenced by hormones, but not necessarily toward the male form. Evidently, the place of the AG in sexual differentiation of dioecious decapods is complex and may differ depending on the particular decapod group.

Acknowledgments

We thank Mr. Alan Poore of Bozman, Maryland, for allowing us to photograph and dissect the gynandromorphic blue crab. Mr. Fred Kern of the Oxford Laboratory kindly photographed the intact animal.

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